THE IMPORTANCE OF REVISIONARY STUDIES IN PLANT SYSTEMATICS[1]

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Our understanding of the diversity and inter-relationships of plant life is based primarily upon the comparative data of revisionary studies. The information in descriptions, keys, and distribution maps, plus the interpretation of relationships based upon these data, all contained within the revisionary study, have contributed much to our attempts to classify and to determine the phylogeny of the plant kingdom. Understanding of these aspects of the plant world is one of the important goals of plant systematics. The success of the past suggests that future attainment of this goal probably cannot be reached without the completion of additional revisionary studies.

Despite the importance of revisions in systematic botany, plant systematics currently is undergoing a metamorphosis in which emphasis is being placed on investigations of the evolutionary process. Although I am personally very interested and excited about all aspects of evolutionary and populational biology, I am concerned about the present status of revisionary studies in plant systematics, especially because it seems that graduate students are being drawn into more experimental and theoretical areas. People earlier (e.g., Robinson, 1923; Just, 1954) have emphasized the need for sustained and increased levels of revisionary efforts, but in view of the present trend toward evolutionary biology I believe that a new statement is needed. The purpose of this paper, therefore, is: (1) to point out the contributions of revisionary studies to plant systematics, (2) to mention the challenges involved with doing good revisionary work, (3) to suggest some innovations in revisionary investigations, and (4) to emphasize the importance of revisionary studies in relationship to the current world ecological situation.

A FEW DEFINITIONS

From a very broad perspective, one can conveniently recognize three types of systematic studies: floristic, experimental (= biosystematic or evolutionary), and revisionary (including synopses and monographs). Many papers actually encompass several of these basic types, and sometimes it

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is difficult to place a particular investigation into one of the three categories. Nevertheless, such a breakdown is useful for our discussion.

Floristic studies attempt to list and describe in various ways the plants of a particular region, from areas as small as state parks or counties to larger areas such as states, regions, nations, or even continents. To describe the plants (even the vascular plants) of a region is a large and difficult job, and the larger the geographic area covered, the more arduous the task becomes. As a result, the portrayal of inter-relationships among taxa in a flora is often somewhat superficial. This is to be expected and is essentially unavoidable.

Experimental investigations, on the other hand, usually focus on some aspect of the evolutionary process, such as hybridization, ecotypic differentiation, or reproductive isolation, to name a few examples. These studies often concentrate on a small number of taxa such as a species complex, and laboratory apparatus of some sort is often used (microscopes, computers, etc.). Most of these studies are not experimental in the strict sense but rather in the broad sense of using equipment that is regularly employed in experimentally-oriented research.[2]

Revisionary studies cover the middle-ground between floristic and experimental approaches by showing detailed relationships among taxa, usually at the generic level and below, based primarily on herbarium investigations, library studies, and field work. Morphology is the primary type of data used, but sometimes other data—such as chromosome numbers or chemical analyses—are included in a revisionary study.

An even finer division can be made by recognizing three types of revisionary studies: synopsis, revision, and monograph. The synopsis is a brief summary of relationships, and usually not all problems in the group have been clarified even by use of library and herbarium facilities. The synopsis, therefore, should be regarded as a pioneering effort. The revision is a more complete statement of relationships among the treated taxa, with full synonymy, lists of excluded taxa, descriptions, keys, distribution maps, citation of representative specimens, and pertinent critical comments. A monograph is essentially the same as a revision except that it has even more information of one sort or another, such as history, chemistry, phytogeography, cytology, or philosophy. In this paper when I speak in general about revisionary studies, I mean all three types of investigations.

Revisionary studies are central to the development of floristic and experimental projects. Floristic work draws heavily on previously published revisions for information on nomenclature, morphology, distribution, and the separation of difficult taxa. Experimental studies also depend strongly

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[2] The term "experimental taxonomy" was originally applied to studies that investigated the nature of species by means of reciprocal transplants (Clements and Hall, 1920); such studies *were* experimental in the strict sense. In the decades after its introduction, however, the term acquired a broader meaning (e.g., Clausen, Keck, and Hiesey, 1941) and thereafter became confused with "biosystematics" (Camp and Gilly, 1943).

upon revisions by focusing on the clarification of relationships that are still not well understood. Difficult taxonomic situations that may lead to experimental studies often result from the evolutionary dynamics of hybridization and/or introgression, inbreeding, and apomixis.

CONTRIBUTIONS OF REVISIONARY STUDIES TO PLANT SYSTEMATICS

I believe revisions to be useful in plant systematics primarily in four ways: (1) as a source of classifications, (2) as an aid to identification, (3) as a source of biological data, and (4) as a stimulus for further study. Each of these uses will be discussed in turn.

The most significant contribution of revisionary studies is as a source of hierarchies of classification. Classifications are fundamental to the growth and development of plant systematics by playing at least three important roles (in part from Warburton, 1967). First, from the classification one can infer ancestral evolutionary relationships (= phylogenies) among all the included taxa, which gives some idea of the patterns of evolution through long periods of time. Second, the classification allows the biological data presented in the revision (see discussion below) to be retrieved more easily because they are ordered in an hierarchical arrangement corresponding to the classification itself. Third, the classification allows for the prediction of unknown attributes of taxa included in the revision. For example, if certain pharmacologically-active compounds are found in one species, it can be predicted that the most closely related species in the classification might have the same or similar compounds.

Another important use of revisions is for identification purposes. Many types of people, such as wildlife specialists, herbarium curators, etc., desire to know the names of particular plants. If no modern flora exists for an area, or if the group in question is not adequately treated in an available flora, then workers will turn to the keys, distribution maps, and descriptions in the revisionary study for help.

The information contained in a revision—in descriptions, distribution maps, and statements on phenology and ecology—represents biological data on what the plants are like, how they differ from each other, where they grow, and when they flower. Many types of systematists—from horticulturists to phytogeographers—as well as other biologists, seek this information. Phytogeographers are so dependent upon up-to-date revisionary studies that very few meaningful phytogeographic interpretations can be made for genera that are not well understood from a revisionary perspective (Axelrod and Raven, 1972; Thorne, 1972). Many additional data such as nomenclature, discussions of generic relationships, and taxonomic history are usually included in revisions, but this information is generally of lesser interest except to floristic and other revisionary workers.

The revision also serves as a stimulus for further study. Because basic relationships are clearly outlined, other workers such as cytologists or anatomists may want to pursue an analysis of the relationships further.

The revision may prove to be very stimulating to an anatomist, for example, even though no specific anatomical problems are mentioned. The interest may develop simply from his having read the descriptions of the different species or having seen their distributional patterns. On the other hand, specific problems for further study may be emphasized deliberately in the paper. For example, a discussion of difficulties of classification brought on by suspected hybridization and introgression might well catch the interest of a cytogeneticist.

REQUIREMENTS FOR GOOD REVISIONARY WORK

Although admitting the value of revisionary studies, some botanists might not realize that significant differences exist in the quality of revisionary work produced. Considerable variations among finished revisions do prevail, however, even to the extent that some studies are so inadequate that they prove nearly worthless for those purposes I mentioned earlier. Asa Gray, almost a century ago (1875), put it this way (p. 353): "Easy as the work may seem, the number of botanists who are able to elaborate a genus and draw up fairly good botanical descriptions is wonderfully small. The thing is quite possible if mere literary compilation is intended; but something more than this is needed."

The general requirements for excellence in revisionary work apply basically to most descriptive sciences and to a lesser degree even to experimental sciences. Many criteria might be formulated for evaluating the ability of a revisionary worker (and, therefore, also the quality of his published revisions), but I have selected six of what to me seem the most important: (1) precision and thoroughness in gathering of comparative data of all types; (2) ability to recognize discontinuities in sets of comparative data (= pattern recognition); (3) ability to relate observed discontinuities in sets of data to the various fixed ranks of the taxonomic hierarchy; (4) precision and thoroughness of description of recognized taxa; (5) precision and thoroughness of documentation in literature, specimen citations, and nomenclature; and (6) precision, thoroughness, and clarity of expression in the final written treatment. These six general criteria must be kept in mind when pursuing each of the three major aspects of revisionary studies: field, library, and herbarium investigations. But in addition to these general criteria, specific requirements for excellence in each of these activities also must be considered.

Although the completion of field investigations is not absolutely essential for good revisionary studies, there is little doubt that all other factors being equal, the more field work a researcher is able to do, the better will be his resultant treatment. The value of field observations for the revisionary worker lies mainly in improving his ability to recognize discontinuities among local populations and to relate the resultant groups to categories in the taxonomic hierarchy. Refined classifications can be produced solely from herbarium material, as has been done by many workers in the past

(e.g., S. F. Blake, B. L. Robinson), but such studies tend to be myopic in their treatment of relationships.

Library investigations are very important primarily because revisionary studies have a strong historical orientation. Not only must past aspects of nomenclature be understood fully, but also the literature must be searched extensively for taxonomic opinions or dispositions that may bear on the present attempts at classification. To be skilled in library work demands traits characteristic of professional botanical bibliographers: knowledge of languages, familiarity with literature on itineraries and biographies of collectors, understanding of abbreviations of older taxonomic literature, familiarity with the *International Code of Botanical Nomenclature*, and—most importantly—patience.

Herbarium investigations likewise are a very important part of the revisionary effort. These center on the core of the revision proper, which is the development of concepts of taxa and their subsequent ranking. It is at this point that the natural ability of the taxonomist must show through. He must have the talent to recognize discontinuities in data sets, or to put this same idea another way, he must have a "taxonomist's eye." The recognition of discontinuities sometimes can be very challenging, especially if the group in question shows unusual patterns of variation. In these cases a strong background in evolutionary theory is most helpful, if not absolutely necessary, to correctly identify apomixis, hybridization, or ecotypic differentiation and to make the proper taxonomic dispositions. Furthermore, to be good in pattern recognition necessitates knowing something about the kinds of data that have been collected and whether or not they have been collected correctly and in sufficient quantity. A good understanding of the morphology of the group in question is therefore essential, as is the full understanding of other types of data, such as anatomy, cytology, or chemistry, that may be available for use.

INNOVATIONS IN METHODS OF REVISIONARY STUDY

As with any aspect of plant systematics, innovations in approaches to revisionary studies must occur periodically or the studies themselves will never approximate their full utility. The basic formats and methodologies for revisionary work have been around since the time of Linnaeus.[3] From that beginning the approaches have remained largely unchanged except for the use of additional types of data on which to base the classifications. Because over 2 centuries have passed since the appearance of the early revisionary literature, it is appropriate at this time to consider if changes might be beneficial.

Unlike most experimental systematic studies, the format for presentation of data in revisionary studies is very rigid. The reason for this rigidity de-

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[3] Although taxonomic studies with "revision" in the title did not appear until the late 19th century, the earlier world floras of Linnaeus and DeCandolle are clearly revisionary in format and perspective.

rives from the objectives or uses of the revision, for which ease of data retrieval is paramount. The descriptions, keys, lists of synonyms, citations of representative specimens, and distribution maps are effective ways to insure accessibility of information. Innovations in methods of revisionary study should therefore be concerned primarily with new ways to develop and process data necessary to fill the revisionary structure, rather than with developing a new structure altogether. Some space-saving changes in structure may be desirable, however, such as the substitution of data matrices for keys and descriptions (Solbrig, pers. comm.).

Teamwork as a means of speeding up completion of revisionary studies has been emphasized by Leenhouts (1968) and by Blair and Turner (1972), and I agree with their suggestions. In the past, some joint ventures have been very successful (e.g., B. L. Robinson and J. M. Greenman; M. Mathias and L. Constance), and these should serve to encourage others to follow suit in the future. It is realized that productive joint ventures rest with compatible personalities that cannot be forced, but perhaps more overtures can be made toward colleagues with whom collaboration might succeed.

The gathering together of library materials is now a much easier task than ever before. This does not mean that interpretation of data is any easier but simply that the relevant publications can be located more quickly through numerous indexes and obtained much faster through copy machines or on microform. Reader-printer machines now available allow for hard-copy to be obtained cheaply and rapidly from microform publications.

The gathering together of herbarium specimens also is much easier than ever before. With the publication of the recent edition of the *Index Herbariorum* (Holmgren and Keuken, 1974) the existence of collections from which loans may be made is now known to all workers, even those in isolated geographic regions. Furthermore, the availability of Inter Documentation Company (Zug, Switzerland) microfiche editions of herbaria from which loans are not permitted (e.g., Linnaean and DeCandolle herbaria) has made examination of these collections almost routine.

In my opinion, one of the most significant innovations in methods of revisionary study will come with the use of machine-assisted operations. Because many of the procedures used in revisionary work deal with data manipulation, data-processing machines are ideally suited for aiding this work. The following paragraphs explain briefly how these machines might be useful in some of the individual procedures.

The preparation of lists of representative specimens during the course of a revisionary study is a laborious, time-consuming, and error-prone task. To speed up this aspect of the work, in our laboratory we have developed a computer program (Meacham and Stuessy, 1974) that allows for specimens to be cited automatically once the data are on machine-readable cards. The details of this program will be reported elsewhere, but I should mention that the procedures for coding of data are so simple that any taxonomist can use the program with almost no prior knowledge of computers. An ad-

ditional step that we have not done, but that has been done already by some workers (Soper, 1964; Gómez-Pompa and Nevling, 1973; Adams, 1974), is plotting specimen localities by computer on a base map.

Another time-saving procedure is use of a flexowriter, which essentially is a typewriter that generates a punched paper (or magnetic) tape at the same time the first manuscript draft is produced. This machine is very useful for the typing of descriptions and other textual portions that are not likely to be highly modified after the initial draft. At the time of final manuscript production, the paper tape is used to produce an edited typescript with no detailed proofreading being necessary.

One more computer procedure that will help make revisionary work more efficient is the preparation of keys directly from descriptions. It remains to be seen whether computers can produce as good a key as a taxonomist can, but it is very clear that preliminary keys can be generated that might be further modified by the worker with a net saving of time. Although this is a complex manipulation for computers, and although we are still a long way from having truly serviceable algorithms, preliminary studies (Hall, 1970; Pankhurst, 1971, 1974; Morse, 1971; Pettigrew and Watson, 1973; Dallwitz, 1974) suggest that some of the difficulties will be overcome soon. This procedure need not involve additional laborious coding of descriptive data either, because once the data from the descriptions are on paper or magnetic tape, as with use of the flexowriter described above, they could be fed with proper conversion into the computer without additional manual coding.

RELATIONSHIP OF REVISIONARY STUDIES TO THE ECOLOGICAL CRISIS

With the growing realization that the world's biota is diminishing at an alarming rate primarily as a result of man's modification of the environment, a new term, the "ecological crisis," has been coined to dramatize this loss of organic diversity. Implicit in this concept is that organisms higher up in the food webs, such as man himself, eventually will be harmed by the loss of diversity at lower trophic levels. Many scientists have recognized this problem (e.g., Iltis, 1967; Fosberg, 1972; Holdren and Ehrlich, 1974), and many books have been written (e.g., Ehrlich, 1968; Johnson, 1970; Matthews, Smith and Goldberg, 1971) that speak to the dilemma and its resolution, at least in part.

Because the present decline in diversity of the world's flora is likely to continue in years ahead, the plant systematist is faced with the responsibility of deciding which types of studies now appear to be most useful or productive, not only in a restricted sense for systematic botany, but also for mankind in general. The plant systematist is in the unique position of possessing considerable knowledge about the world's flora, and therefore presumably also in a good position to evaluate the kinds of studies that are important to stress at this time. Because of personal biases, different plant

systematists might give different values to the various kinds of studies. We do, it is true, need more experimental studies to learn as much as possible about the evolutionary process before the key intermediate taxa become extinct. Likewise, we also need an increased effort in floristic studies so that at least we will have some idea of what plants grow in particular regions before the flora is decimated.

Although respecting these different viewpoints, I believe that the revisionary study is the type of investigation most needed at this time. Reasons for this position lie principally with my view of the revision as being central to all facets of systematic botany. Although floristic treatments sketch relationships among the included taxa, the depth of understanding in this type of study is necessarily limited and is not best suited for helping us understand phylogenetic and phytogeographic relationships of the groups concerned, nor for understanding mechanisms of speciation that have prevailed. Moreover, the floristic study may not clarify fully the nomenclatural problems, so that the names for the taxa themselves may not even be correct.[4] Experimental studies on small groups of species are also needed at this time, but unless we have an accurate understanding of the basic relationships of most plant species, it will be impossible to extrapolate from these few in-depth studies on the process of evolution to the probable patterns of evolution in other groups of taxa. Therefore, to help document the world's flora before it vanishes, I agree with Turner (1971) that plant systematists should give emphasis to revisionary investigations and, in particular, to encouraging students to pursue these endeavors.

Because of the above assessment of the importance of revisionary studies in systematic botany, especially at this point in time, I believe that we should give attention to the support of field endeavors that bear on these efforts. Two types of collecting programs will give maximum return in this direction: (1) those completed by the revisionary worker himself in any region of the globe and (2) those completed by the floristic worker in very obscure regions of the earth as yet untouched markedly by European man (e.g., Amazon basin of South America) or in areas in danger of immediate and irreversible destruction (e.g., Mexican highlands). The revisionary worker is in the best position to make critical collections and observations that will allow the most significant data to be obtained from his plant materials in the future. The floristic worker in obscure or threatened regions will serve the valuable function of collecting at least some materials that can be worked up at a later date as part of a revisionary investigation. I believe that both types of field programs are urgently needed.

CONCLUSION

The previous discussions have attempted to show that revisionary studies

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[4] I would agree that detailed and critical floras (of which few exist) avoid most of these limitations, but I contend that such works are basically revisionary in character because of their depth of coverage.

play a very important role in plant systematics. I have tried to indicate that being a productive and excellent revisionary worker involves many challenges, including acquiring knowledge in several diverse areas—from botanical bibliography to evolutionary theory. Such challenges should be pointed out to graduate students so that a larger number of them will become stimulated to pursue these endeavors. With the world's flora disappearing at an increasing rate, we need as many people as possible studying basic plant relationships before the plants themselves are completely extirpated. The hope is that we can obtain enough detailed information about the flora to give us a foundation for future studies leading to at least a partial understanding of phylogeny and evolutionary processes in the plant kingdom.

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